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European plants with C_4 photosynthesis: geographical and taxonomic distribution and relations to climate parameters

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A survey of C_4 plants in Europe was performed with 216 species based on information in the literature and new studies. C_4 species were found in 10 families: the eudicots Amaranthaceae, Chenopodiaceae, Euphorbiaceae, Molluginaceae, Nyctaginaceae, Polygonaceae, Portulacaceae and Zygophyllaceae and the monocots Cyperaceae and Poaceae. The majority of the C_4 species belong to four families, Amaranthaceae (23), Chenopodiaceae (65), Cyperaceae (27) and Poaceae (88). In central and southern Europe, the abundance of native C_4 plants varied between 44 and 88% of total C_4 plants occurring, the rest being invasive C_4 species. The occurrence of total C_4 species, C_4 monocots and C_4 Chenopodiaceae was assessed for five major phyto-geographical regions of Europe (north-west, north-east, central, south-west, and south-east). The abundance of C_4 plants of total C_4 dicots, C_4 Chenopodiaceae, total C_4 monocots, C_4 Poaceae and C_4 Cyperaceae was related to the climatic variables of annual mean daily temperature, annual precipitation and DeMartonne's aridity index. The abundance of total C_4 plants decreases with increasing temperature and expression of aridity (decreasing aridity index) and is not correlated with precipitation. The abundance of total C_4 dicots and C_4 Chenopodiaceae is correlated with precipitation and aridity but not temperature, whereas the abundance of total C_4 monocots, C_4 Poaceae and C_4 Cyperaceae is correlated with temperature and aridity but not precipitation. *Botanical Journal of the Linnean Society*, 2010, **163**, 283–304.

ADDITIONAL KEYWORDS: Amaranthaceae – aridity – carbon isotope ratios – Chenopodiaceae – Cyperaceae – phytogeography – Poaceae.

INTRODUCTION

Among plants we find three main modes of photosynthesis. In C_3 photosynthesis, CO_2 is fixed directly by the oxygen sensitive ribulose-bis-phosphate carboxylase/oxygenase (RUBISCO) and the first stable fixation product is the C_3 compound phosphoglyceric acid. In C_4 photosynthesis and crassulacean acid metabolism (CAM), CO_2 is first fixed by the oxygen insensitive phospho*enol*pyruvate carboxylase (PEPC) and the first stable fixation product is the C_4 compound malic acid. Both are water-saving mechanisms, functioning by concentrating CO_2 internally (Lüttge, 2002). In CAM, CO_2 is fixed by PEPC during the dark period, the malic acid (anion: malate) produced is stored in the vacuoles and remobilized in the light period to generate CO_2 by decarboxylation for refixation via RUBISCO and assimilation in the Calvin cycle. In C_4 photosynthesis, CO_2 is fixed by PEPC in the light

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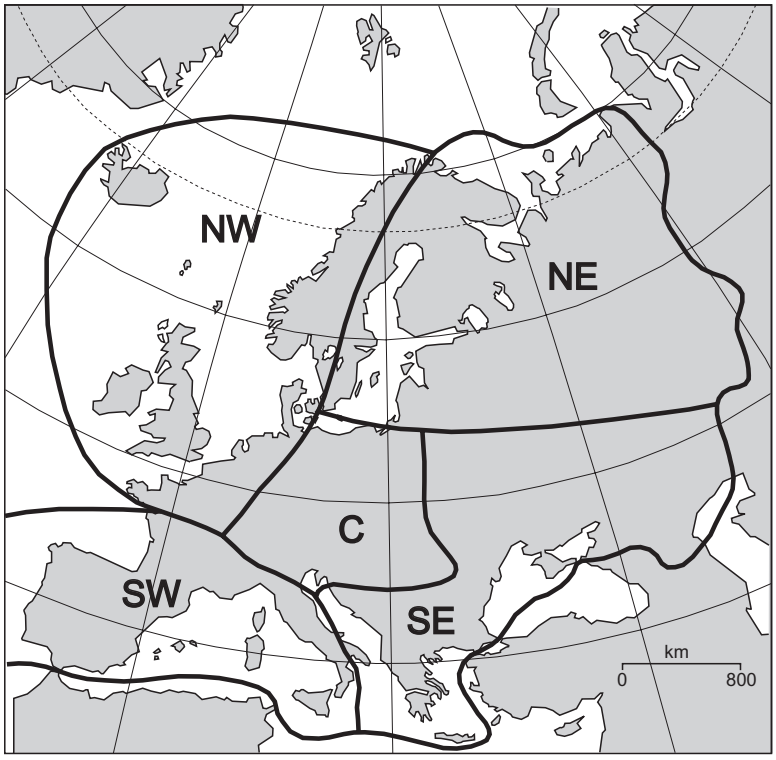

Figure 1. The area of Europe covered in the present study and the distinction of five main regions [north-west (NW), north-east (NE), central (C), south-west (SW) and south-east (SE) Europe] used in the discussion of data.

mainly in peripheral green tissue (mesophyll tissue), the malate produced is transported to green cells of bundle sheaths where it is decarboxylated and the CO_2 produced is refixed and assimilated via RUBISCO. According to the acting decarboxylating enzymes, i.e. NAD-dependent malic enzyme, NADP-dependent malic enzyme and phospho*enol*pyruvate carboxykinase, we distinguish three different metabolic types of C_4 plants (NAD-ME, NADP-ME and PEPCK type). Because PEPC has a *c*. 60-fold higher affinity for CO_2 than RUBISCO, this process overall results in an approximately 6- to 8-fold increase in the CO_2 concentration in the bundle sheaths compared with the external atmosphere.

As PEPC fixes HCO_3^- instead of free CO_2, and as HCO_3^- is enriched in ^{13}C compared with free CO_2, PEPC shows a much smaller discrimination to $^{13}CO_2$ (i.e. 2‰) than RUBISCO (i.e. *c*. 27‰) (Ziegler, 1994). This allows distinction of CAM plants and C_4 plants from C_3 plants by analyses of carbon isotope ratios ($\delta^{13}C$), which are in the range of –9 to –17‰ for C_4 plants, –11 to –32‰ for CAM plants and –22 to –30‰ for C_3 plants. Several additional traits, such as anatomical characteristics and enzyme activities, are used to identify C_4 plants. Although it was found in some species that, in principle, C_4 photosynthesis may occur in particularly compartmented single individual cells of Chenopodiaceae (Edwards, Franceschi & Voznesenskaya, 2004; Akhani *et al*., 2005; Voznesenskaya *et al*., 2001, 2005b; Park *et al*., 2009), a conspicuous anatomical trait of C_4 plants is the so-called Kranz anatomy, in which the green cells cooperating in C_4 photosynthesis (as mentioned above) are differentiated into the green mesophyll tissue and the bundle sheaths.

Climate has a profound effect on the performance of each of the three modes of photosynthesis and, consequently, natural variations in environmental parameters result in different ecological distributions of plants with the three photosynthetic pathways. It is known that plants of these photosynthetic types, in addition to biochemical and physiological differences, exhibit distinct ecological characteristics (Black, 1973; Ehleringer & Monson, 1993; Ehleringer, Cerling & Heliker, 1996; Schulze *et al*., 1996). The distribution patterns of C_3, C_4 and CAM plant species in relation to climatic variables can provide direct evidence for the environmental conditions that favour a particular photosynthetic pathway. As C_4 photosynthesis is a CO_2-concentrating mechanism, it allows plants to perform well even when stomata need to be partially closed to reduce transpiratory loss of water, so that this is a biochemical adaptation to water stress. Therefore, the abundance of C_4 species is highly correlated with climatic factors, such as temperature, precipitation and the degree of aridity. It seems likely that different C_4 taxa among the grasses, sedges and dicotyledons

Table 1. Ranges of numbers of C_4 species and related %-values in brackets from Figures 4, 8 and 9 in relation to geographical areas of Europe as delineated in Figure 1

	North-west	North-east	Central	South-west	South-east
All C_4 species (% of total vascular species)	0–18 (0/1.2)	0–15 (0/1.0)	26–50 (1.1/2.1)	39–115 (5.6/2.4)	45–94 (1.9/4.0)
All C_4 monocotyledons (% of total C_4 species)	0–11 (0/61.6)	0–9 (0/100.0)	13–29 (50.0/61.7)	24–71 (61.5/67.6)	23–45 (60.0/66.2)
All C_4 Chenopodiaceae (% of total C_4 species)	0–3 (0/14.0)	0–11 (0/19.0)	2–8 (7.4/18.0)	1–20 (11.0/30.0)	6–46 (27.0/42.0)
All annual C_4 species	0–14 (0/82.4)	1–15 (100)	25–42 (96.2/84.0)	24–70 (61.5/60.9)	35–70 (70.0/74.5)
All perennial C_4 species	0–6 (0/46.2)	0 (0)	1–14 (3.8/22.2)	15–45 (38.5/39.1)	6–24 (13.3/35.3)
All native C_4 species	0–13 (0/76.5)	1–10 (100.0/66.7)	13–32 (72.2/68.1)	17–64 (43.6/55.7)	39–83 (78.0/88.3)
All invasive C_4 species	0–5 (0/27.8)	0–5 (0/33.3)	10–19 (38.5/38.0)	12–51 (25.0/44.3)	11–21 (11.7/29.6)

(Teeri & Stowe, 1976; Stowe & Teeri, 1978) and taxa belonging to different malate decarboxylation types (Hattersley, 1983; Ehleringer *et al*., 1996; Schulze *et al*., 1996) have different reactions to climatic factors and therefore specific patterns of phytogeographical distribution.

Geographical occurrence and distribution in relation to climate of plants with C_4 photosynthesis have been studied across the world (Black, 1971; Berry, 1993), in North America (Teeri & Stowe, 1976; Stowe & Teeri, 1978; Teeri, Stowe & Livingstone, 1980), Africa (Vogel, Fuls & Ellis, 1978; Tieszen *et al*., 1979; Ellis, Vogel & Fuls, 1980; Hesla, Tieszen & Imbamba, 1982; Batanouny, Stichler & Ziegler, 1988; Schulze *et al*., 1996), Australia (Hattersley, 1983; Takeda *et al*., 1995), Central Asia (Gamaley *et al*., 1972; Gamaley, 1985; Pyankov, Vakhrusheva & Burundukova, 1986; Pyankov *et al*., 1992a, b, 1997, 2000a; Pyankov & Molotkovskii, 1992, 1993; Pyankov & Mokronosov, 1993; Pyankov & Vakhrusheva, 1989; Redman, Yin & Wang, 1995), Japan (Okuda & Furukawa, 1990; Ueno & Takeda, 1992) and the Middle East (Shomer-Ilan, Nissenbaum & Waisel, 1981; Akhani, Trimborn & Ziegler, 1997). Relevant studies in Europe were performed by Doliner & Jolliffe (1979), Collins & Jones (1985), Mateu (1992, 1993), Kalapos, Baloghné-Nyakas & Csontos (1997) and Ziegler & Trimborn (2000).

The aim of the present study was, first, to update these surveys and to provide a checklist of C_4 plants of Europe as complete as possible at present based on evaluation of the literature and on new analyses, especially of $\delta^{13}C$-values and C_4 typical anatomical traits (Kranz anatomy) of samples obtained in the field and from herbaria. As the abundance of C_4 plants and C_4 species reflects climate conditions, the list presented in the Appendix to this contribution should provide a firm basis for observations of potential changes during the future development of global (including European) climate conditions. In this context, it was a second aim to analyse the geographical distribution patterns of C_4 species from the main families of Chenopodiaceae, Poaceae and Cyperaceae, in which we also wanted to test the hypothesis that abundance of C_4 plants is correlated to the degree of aridity in Europe, although regions with extreme aridity (deserts) do not occur on the continent. We keep Chenopodiaceae as a separate family and do not integrate it in Amaranthaceae as proposed recently (APG II, 2003; Kadereit, 2008; APG III, 2009)[1]. Thirdly, we evaluated the proportions of annual and perennial and of native and invasive C_4 plants in the phytogeographical regions of Europe to demonstrate differences in their abundance under the impact of climate. Overall, this work allows us to suggest a specific performance capacity of different taxonomic and functional groups of C_4 species under the various climatic conditions in Europe, which will be useful in predicting vegetation changes during potential climatic changes.

MATERIAL AND METHODS

PHYTOGEOGRAPHICAL SPECIES DISTRIBUTION

The area of Europe covered in the present study is shown in Figure 1 and five phytogeographical regions

[1]Editor's note: It is journal policy to use only those family names recognized in APG III (2009), but, given the circumstances relating to the authorship of this paper, an exception is made here and the authors have been given permission to use Chenopodiaceae in its traditional sense in addition to Amaranthaceae (APG III combines these two families as Amaranthaceae).

are also delineated. The data obtained for different areas and countries are superimposed on the respective parts of the map in Figures 4, 8 and 9. To facilitate overview and comprehension, the ranges of values characteristic for the five regions are listed in Table 1, namely north-west, north-east, central, south-west and south-east Europe. After species were identified as C_4 species (see below), their distribution and status in each region as native or weedy and invasive was obtained from Flora Europaea (Tutin *et al*., 1964–1980, 1993).

The climatic data characterizing the phytogeographical regions and selected for analysis of C_4 plant distribution data were taken from Müller (1982). Values of climatic variables were selected from the set of meteorological stations in each region. The aridity index according to DeMartonne (1926a, b) is given by $P/(T + 10)$ (mm/°C), where P is annual precipitation (mm) and T is annual mean temperature (°C), hence the numerical value of the index is reversely correlated with the actual degree of aridity.

Classification of species as C_4 plants

The classification of species as C_4 plants was based on data of the literature and new results, especially $\delta^{13}C$-analyses, biochemical studies and anatomical traits, mainly Kranz anatomy. The literature sources for the checklist of European C_4 plants were Doliner & Jolliffe (1979), Collins & Jones (1985) and Mateu (1992, 1993), for Chenopodiaceae, Winter (1981), Pyankov *et al*. (1992a, b, 1997) and Akhani *et al*. (1997), for Euphorbiaceae Batanouny, Stichler & Ziegler (1991), for Poaceae Ziegler *et al*. (1981), Batanouny *et al*. (1988), Hattersley & Watson (1992) and Schulze *et al*. (1996) and for the Cyperaceae Ueno, Takea & Murata (1986), Uneo, Takea & Maeda (1988), Ueno & Takeda (1992) and Li (1993). Newly identified C_4 species were determined in plants collected during expeditions to Central Asia, Mongolia and Uzbekistan (Vladimir Pyankov) and in samples obtained from herbarium specimens of the Bayerische Botanische Staatssammlung, Munich, Germany (V. Pyankov, H. Ziegler) and the Komarov Botanical Institute, St Petersburg, Russia (V. Pyankov). Vouchers of the plants are deposited at the Bayerische Botanische Staatssammlung and the Komarov Botanical Institute.

$\delta^{13}C$ analysis

Carbon isotope ratios were determined on dried samples, mostly of leaves, using the standard procedure to obtain $\delta^{13}C$-values relative to Pee Dee Belemnite (see Schulze *et al*., 1996).

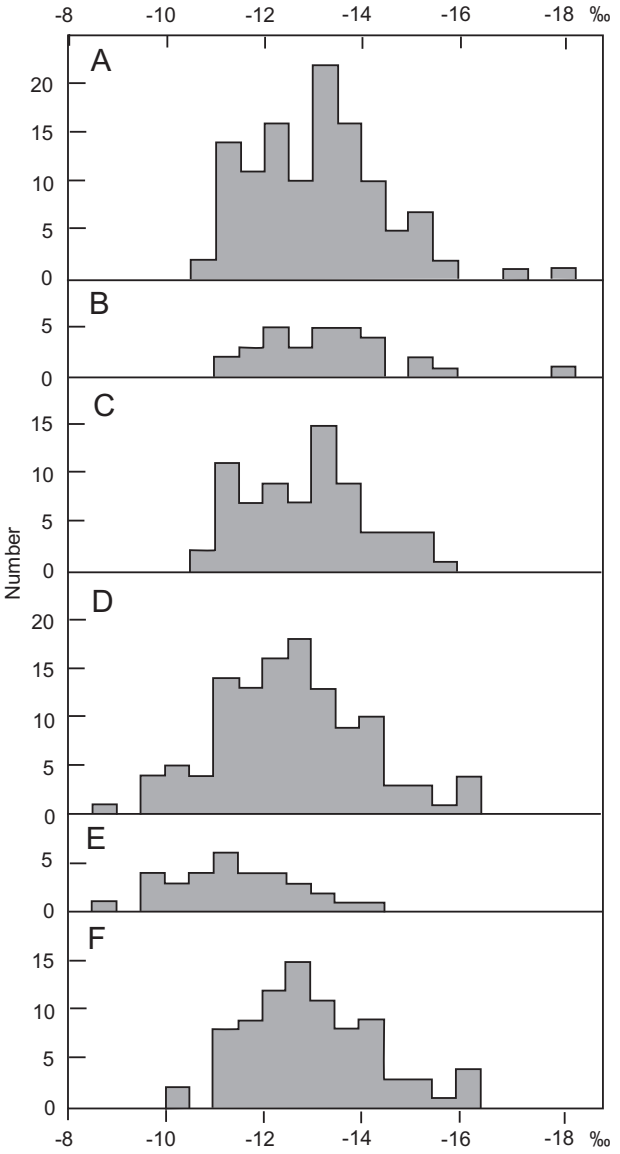

Figure 2. Range of $\delta^{13}C$-values related to the number of species analysed of (A) all C_4 dicotyledons, (B) all C_4 Amaranthaceae, (C) all C_4 Chenopodiaceae, (D) all C_4 monocotyledons, (E) all C_4 Cyperaceae and (F) all C_4 Poaceae.

Correlation analysis

Relations of distribution and abundance of C_4 plants to climatic variables were assessed by linear correlation analysis and are presented together with the correlation coefficients, r.

RESULTS

The European C_4 flora

The data of the tables and figures in this study are based on a survey of 216 species (see Appendix for detailed information relating to these species). The

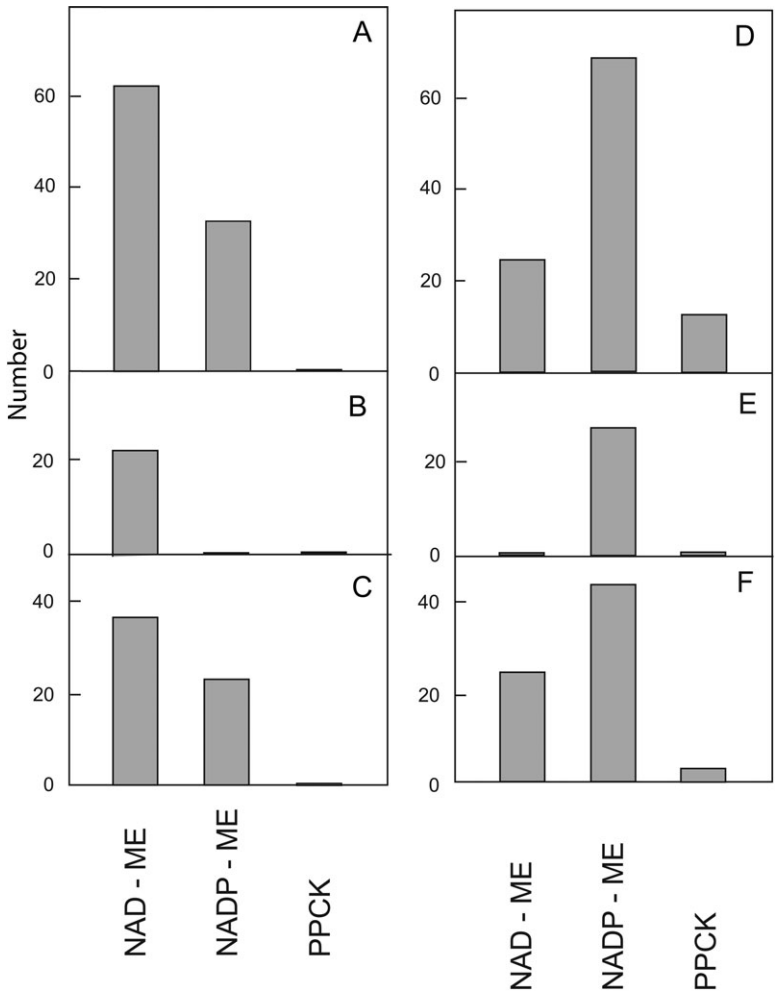

Figure 3. Modes of malate decarboxylation in the C_4 pathway by NAD-dependent malic enzyme (NAD-ME), NADP-dependent malic enzyme (NADP-ME) and phospho*enol*pyruvate carboxykinase (PPCK) related to the number of species analysed of (A) all C_4 dicotyledons, (B) all C_4 Amaranthaceae, (C) all C_4 Chenopodiaceae, (D) all C_4 monocotyledons, (E) all C_4 Cyperaceae and (F) all C_4 Poaceae.

Table 2. Correlation coefficients, *r*, of the linear regressions of the correlations of numbers of C_4 plants of different taxonomic groups recorded to climate parameters (see also Figs 5–7).

	Annual mean daily temperature	Annual precipitation	Annual aridity index
All C_4 plants	0.611	–0.210	–0.517
Dicotyledons			
All C_4 dicotyledons	0.232	–0.429	–0.574
C_4 Chenopodiaceae	0.135	–0.471	–0.567
Monocotyledons			
All C_4 monocotyledons	0.693	–0.082	–0.417
C_4 Poaceae	0.649	–0.100	–0.415
C_4 Cyperaceae	0.739	–0.050	–0.387

Figure 4. Geographical distribution in Europe of (A) total C_4 species (numbers with % C_4 species of total vascular species of the respective area in brackets), (B) total C_4 monocotyledons (numbers with % C_4 monocotyledons of total C_4 species in brackets) and (C) total C_4 Chenopodiaceae (numbers with % C_4 Chenopodiaceae of total C_4 species in brackets).

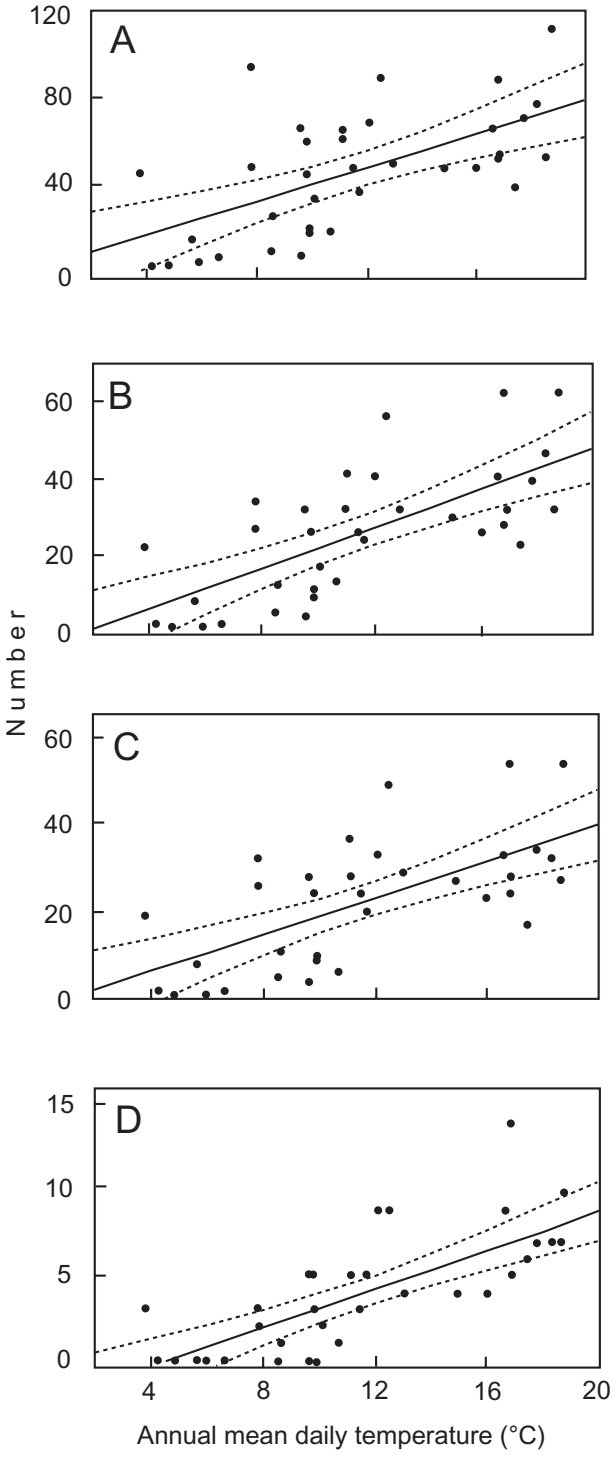

Figure 5. Correlation of the number of plants recorded to annual mean daily temperature of (A) all C_4 plants, (B) all C_4 monocotyledons, (C) all C_4 Poaceae and (D) all C_4 Cyperaceae. Solid lines: linear regressions; dotted lines: 95% confidence limits.

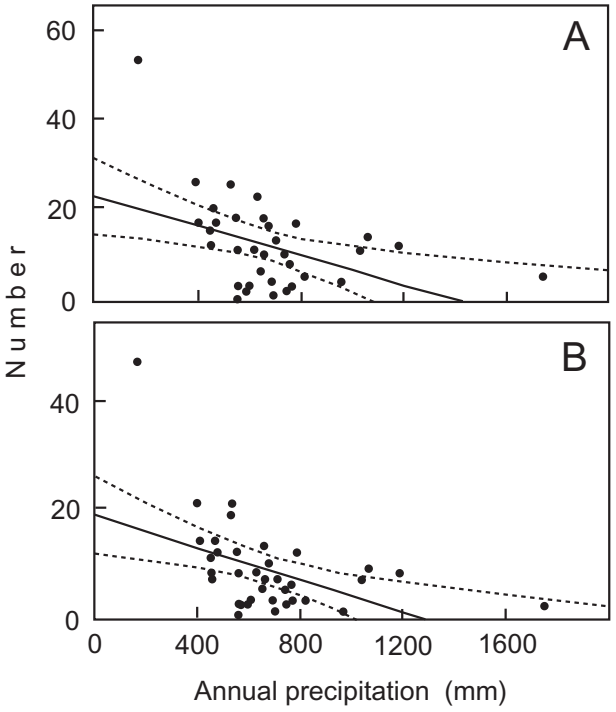

Figure 6. Correlation of the number of plants recorded to annual precipitation of (A) all C_4 dicotyledons, (B) all C_4 Chenopodiaceae. Solid lines: linear regressions; dotted lines: 95% confidence limits.

216 species comprise 101 dicotyledons (among which are 65 Chenopodiaceae) and 115 monocotyledons (88 Poaceae and 27 Cyperaceae). Hence, the contribution of dicotyledons and monocotyledons to the European C_4 flora is not very different, with only *c*. 15% more monocotyledons; Chenopodiaceae and Poaceae are the major C_4 families.

Biochemical characteristics

For the major groups of taxa, Figure 2 shows the range of $\delta^{13}C$-values in relation to the number of species analysed. The distribution for all dicotyledons together and Chenopodiaceae separately is similar, attributable to the fact that Chenopodiaceae make the major contribution to C_4 dicotyledons. The distribution for all monocotyledons is dominated by that of Poaceae, which make the major contribution there. It is seen that the distribution peaks are at a little less negative $\delta^{13}C$-values for the monocotyledons/Poaceae (–12.5 to –13‰) than for the dicotyledons/Chenopodiaceae (–13 to –13.5‰). It is noteworthy then that, by contrast to the dicotyledons, the monocotyledons also show $\delta^{13}C$-values less negative than –10.5‰.

In the C_4 metabolic cycle, daytime malate decarboxylation may be mediated by NAD-dependent malic enzyme (NAD-ME) or by NADP-dependent malic enzyme (NADP-ME) or by phospho*enol*pyruvate carboxykinase (PEPCK). Figure 3 shows the occurrence

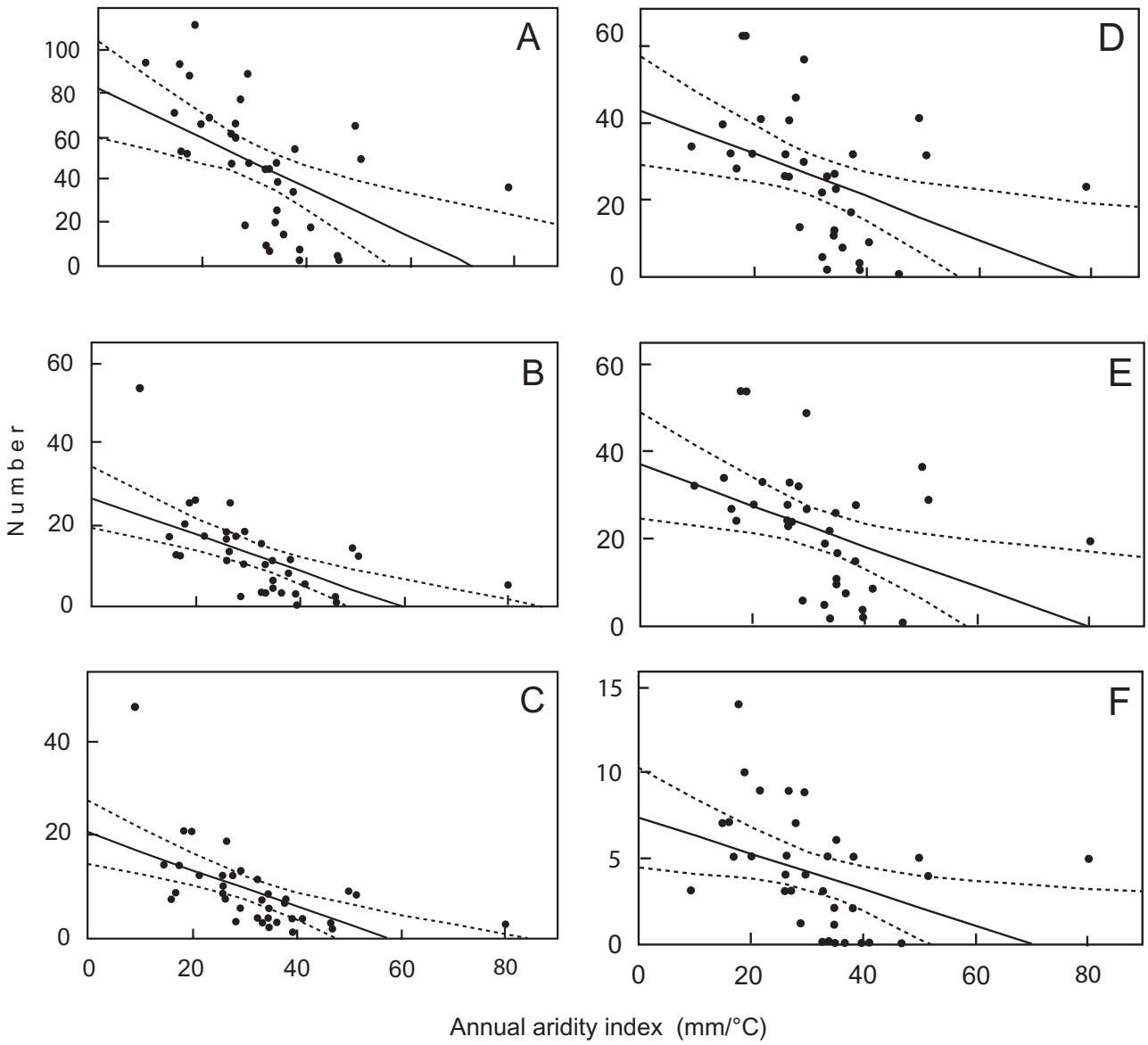

Figure 7. Correlation of the number of plants recorded to annual DeMartonne's aridity index of (A) all C_4 plants, (B) all C_4 dicotyledons, (C) all C_4 Chenopodiaceae, (D) all C_4 monocotyledons, (E) all C_4 Poaceae and (F) all C_4 Cyperaceae. Solid lines: linear regressions; dotted lines: 95% confidence limits.

of the respective modes among the C_4 species of Europe. The PEPCK type only occurs in C_4 monocotyledons. Among European C_4 plants, it is rare and occurs only in 13 species of Poaceae. Among the C_4 dicotyledons and Chenopodiaceae separately, the NAD-ME type is more common than the NADP-ME type, whereas among the C_4 monocotyledons the latter is more dominant.

Geographical distribution of European C_4 plants and relations to climatic factors

The geographical distribution of European C_4 plants is depicted in the maps of Figure 4A–C, where the absolute numbers of species occurring are written in, together with some relative evaluations (% values). For the ranges of values see Table 1.

The absolute number of C_4 species and the percentage they represent of total species of vascular plants are quite low in the northern regions (north-west and north-east), but increase considerably in the centre (central) and especially in the southern regions (south-west and south-east). Similar trends are revealed when the C_4 Poaceae and the C_4 Chenopodiaceae are considered separately. In central and south-west Europe, C_4 Poaceae dominate, but in south-east Europe, C_4 Chenopodiaceae can locally

attain similar numbers. West to east gradients, which might reflect oceanic and continental influences, respectively, are not pronounced.

In order to investigate potential climatic relationships of the conspicuous north–south gradient of distribution, correlations were calculated between the occurrence of C_4 plants of the major taxonomic groups and three climatic parameters, namely annual mean daily temperature, annual precipitation and the aridity index. For the better correlations, curves are presented in Figures 5–7 and the linear regression coefficients of all correlations are presented in Table 2. All groups show a negative correlation with the aridity index, i.e. they are more abundant at higher aridity, although this correlation is only weak for Cyperaceae and the other monocots. However, the aridity index comprises both precipitation and temperature, and there is a conspicuous difference between dicots and monocots with respect to these two parameters. The abundance of C_4 monocots correlates with temperature but not with precipitation, whereas that of the C_4 dicots correlates with precipitation and not with temperature.

Annual and perennial C_4 species of Europe

The area-related abundance of annual and perennial C_4 plants, respectively, is depicted in the maps in Figure 8A and B, where the absolute numbers of plants occurring are written in, together with their percentage contribution to the total C_4 flora. For ranges of values, see Table 1. The numbers of annual C_4 plants in all regions are larger than those of perennial C_4 plants. In the north-east, no perennial C_4 plants occur. Towards the south, with an overall increase of C_4 plants, there are also high numbers of perennial C_4 plants, the highest abundance of them being in the south-west.

Native and invasive C_4 species of Europe

The area-related abundance of native and invasive C_4 plants, respectively, is depicted in the maps in Figure 9A and B, where the absolute numbers of plants occurring are written in, together with their percentage contribution to the total C_4 flora. For ranges of values, see Table 1. In all regions, native C_4 plants dominate. However, invasive species reach considerable numbers in central Europe and in the south. They reach their highest potential in the south-west.

DISCUSSION

C_4 photosynthesis is a biochemical mechanism of a special mode of photosynthesis for concentrating CO_2 internally. Therefore, C_4 plants can still operate well with partially closed stomata. They generally have high water use efficiency (Black, 1973). Hence, the observation that C_4 plants are more abundant in central and southern Europe (Fig. 4, Table 1) and the correlation of the abundance of C_4 plants with the expression of aridity, as borne out by the data presented (low aridity index, Fig. 7, Table 2) confirm the hypothesis posed in the Introduction that the relative degree of aridity also determines phytogeographical distribution of C_4 plants in Europe. The highest abundance of C_4 plants is not, however, observed in the south-east, where one might expect a floristic pressure from the Eurasian steppes, although the high abundance of C_4 Chenopodiaceae is remarkable there.

It is intriguing that monocots respond much more to the temperature factor and, conversely, dicots to the precipitation factor of the aridity index (Table 2). Grasses and sedges (Poaceae, Cyperaceae) often possess morphological and anatomical traits, such as narrow rolled leaves and epidermal cavities protecting stomata under stress of low water availability and thick cuticles. These contribute to controlling transpiratory water loss when water is limiting, whereas they do not help to avoid temperature stress. In contrast, lower transpiration reduces transpirational cooling and this increases temperature stress. Thus, the stress adaptive C_4 mode should prove to be less in demand in relation to water stress and more important in relation to temperature stress, which may explain why the abundance of C_4 monocots increases more in response to temperature than precipitation. Conversely, broad-leaved dicots may suffer more immediate stress as a result of transpiration when precipitation is low and the abundance of C_4 dicots responds more directly to transpiration. In comparisons between C_3 plants when all other external and internal parameters are similar, one can take more negative $\delta^{13}C$-values as an indication of higher transpiration and lower water use efficiency (Farquhar, Ehleringer & Hubick, 1989a; Farquhar *et al*., 1989b; Guehl *et al*., 2004). If we may also apply this to the comparison between C_4 plants, the observation that there were $\delta^{13}C$-values for C_4 monocots less negative than –10.5‰ which did not occur among C_4 dicots (Fig. 2) would agree with a higher transpiration and lower water use efficiency of the latter.

The data show that there are more C_4 annuals than C_4 perennials (Fig. 8, Table 1). C_4 photosynthesis is frequently observed to allow high productivity over short periods of time. Therefore, this mode of photosynthesis may be a trait particularly providing higher fitness to annuals. This may be one of the reasons for the observation that, although some perennial and also shrubby woody C_4 species exist, there are no real C_4 trees (Sage, Li & Monson, 1999; Sage & Pearcy, 2000).

Native C_4 plants are still more abundant in Europe than invasive C_4 plants (Fig. 9, Table 1). However, the number of invasive C_4 plants is high, i.e. up to 40%.

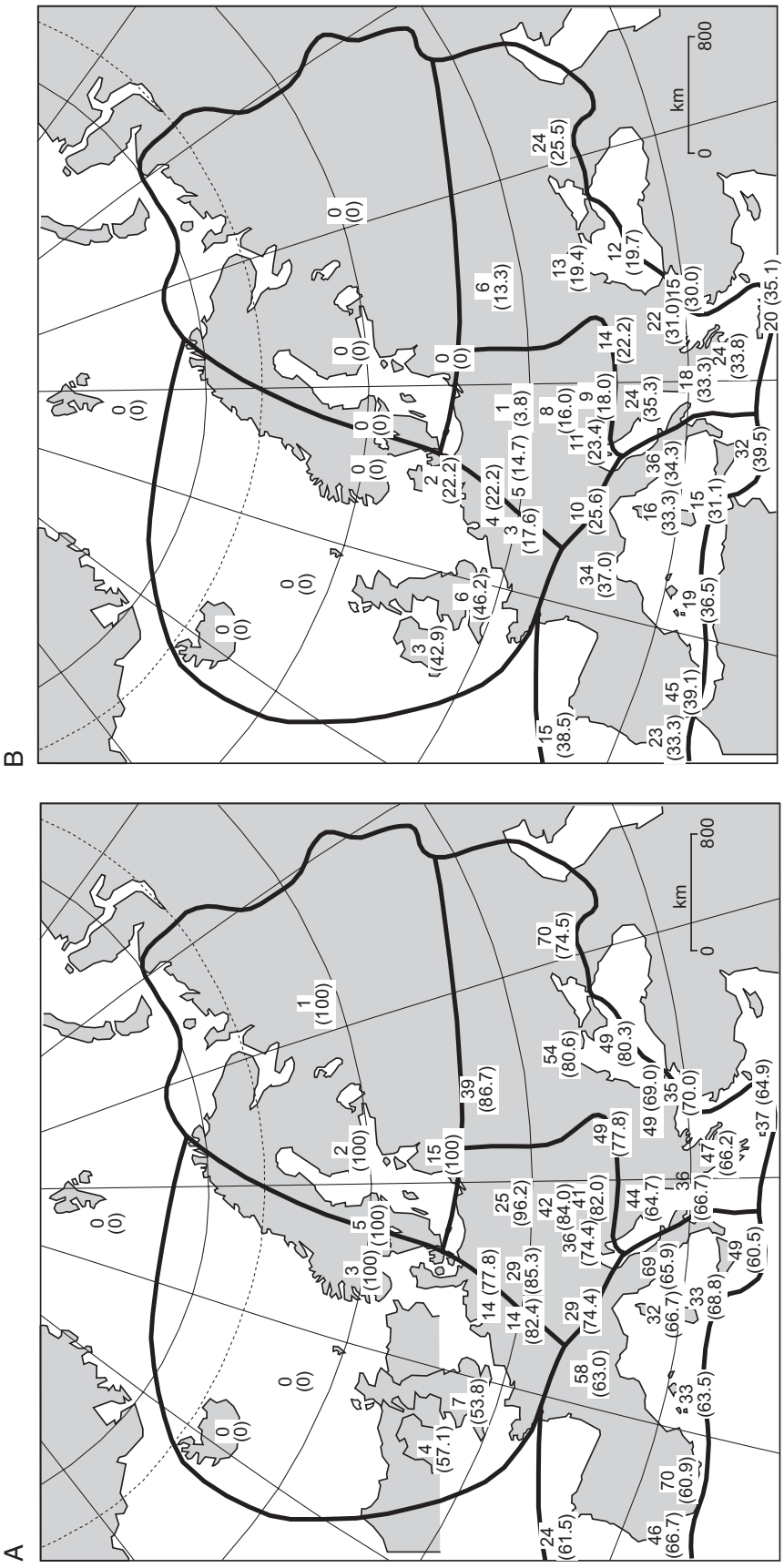

Figure 8. Geographical distribution in Europe of (A) all annual C_4 plants and (B) all perennial C_4 plants with % of total C_4 plants in brackets.

Figure 9. Geographical distribution in Europe of (A) all locally native C_4 plants and (B) all invasive C_4 plants with % of total C_4 plants in brackets.

In general, invasive species often possess high phenotypic plasticity, broadly defined as the ability to alter their morphology and physiology in response to varying environmental conditions, which allows them to occupy a wide range of new environments (Funk, 2008). It is intriguing that the number of invasive C_4 plants is particularly high in the south-west and not in the south-east. Most of the diversification of C_4 traits occurred in central Asian and Middle Eastern deserts in a wide range of habitats from hyper-saline to extremely arid conditions, and this is a radiation centre of C_4 plants in the Old World (Sage, 2004; Akhani, 2006). Thus, on the one hand, in south-eastern Europe one would expect a higher floristic pressure of invasion from the Eurasian steppes rich in C_4 species, and, hence, a larger number of invasive C_4 species. On the other hand, one should never neglect the strong anthropogenic influence in the spreading of neophytes around the world in the past and in the present. Thus, intensive maritime traffic might explain the particular abundance of invasive C_4 species in the south-west area in this survey. Future developments depend on many interacting factors and are difficult to predict, but anthropogenic mobility and changes of climate may contribute to them.

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REFERENCES

Akhani H. 2006. Biodiversity of halophytic and sabkha ecosystems in Iran. In: Khan A, Böer B, Kust GS, Barth H-J, eds. *Sabkha ecosystems: vol. II: West and Central Asia*. New York: Springer, 71–88.

Akhani H, Ghasemkhani M. 2007. Diversity of photosynthetic organs in Chenopodiaceae from Golestan National Park (NE Iran) based on carbon isotope composition and anatomy of leaves and cotyledons. *Nova Hedwigia* Suppl. **131:** 265–277.

Akhani H, Ziegler H. 2002. Photosynthetic pathways and habitats of grasses in Golestan National Park (NE Iran), with an emphasis on the C-4-grass dominated rock communities. *Phytocoenologia* **32:** 455–501.

Akhani H, Trimborn P, Ziegler H. 1997. Photosynthetic pathways in Chenopodiaceae from Africa, Asia and Europe with their ecological, phytogeographical and taxonomical importance. *Plant Systematics and Evolution* **206:** 187–221.

Akhani H, Barroca J, Koteeva N, Voznesenskaya EV, Franceschi VR, Edwards GE, Ghaffari SM, Ziegler H. 2005. *Bienertia sinuspersici* (Chenopodiaceae): a new species from southwest Asia and discovery of a third terrestrial C_4 plant without Kranz anatomy. *Systematic Botany* **30:** 290–301.

Akhani H, Edwards G, Roalson EH. 2007. Diversification of the Old World Salsoleae *s.l.* (Chenopodiaceae): molecular phylogenetic analysis of nuclear and chloroplast datasets and a revised classification. *International Journal of Plant Science* **168:** 931–956.

Akhani H, Lara MV, Ghasemkhani M, Ziegler H, Edwards GE. 2009. Does *Bienertia cycloptera* with the single-cell system of C-4 photosynthesis exhibit a seasonal pattern of $\delta^{13}C$ values in nature similar to co-existing C-4 Chenopodiaceae having the dual-cell (Kranz) system? *Photosynthesis Research* **99:** 23–36.

APG II. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Botanical Journal of the Linnean Society* **141:** 399–436.

APG III. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society* **161:** 105–121.

Batanouny KH, Stichler W, Ziegler H. 1988. Photosynthetic pathways, distribution and ecological characteristics of grass species of Egypt. *Oecologia* **75:** 539–548.

Batanouny KH, Stichler W, Ziegler H. 1991. Photosynthetic pathways and ecological distribution of *Euphorbia* species in Egypt. *Oecologia* **87:** 565–569.

Berry JA. 1993. Global distribution of C_4 plants. *Carnegie Institution Year Book* **92:** 66–69.

Black CC. 1971. Ecological implications of dividing plants into groups with distinct photosynthetic production capacity. *Advances in Ecological Research* **7:** 87–114.

Black CC. 1973. Photosynthetic carbon fixation in relation to net CO_2 uptake. *Annual Review of Plant Physiology* **24:** 253–286.

Bruhl JJ, Wilson KL. 2007. Towards a comprehensive survey of C3 and C4 photosynthetic pathways in Cyperaceae. *Aliso* **23:** 99–148.

Carraro L, Patrignani G, Onelli E, Orsenigo M. 1999. Leaf morphology and carbon isotope discrimination values in eyebane (*Euphorbia maculata* L.). *Plant Biosystems* **133:** 55–61.

Collins RP, Jones MB. 1985. The influence of climate factors on the distribution of C_4 species in Europe. *Vegetatio* **64:** 121–129.

DeMartonne E. 1926a. Aérisme et indice d'aridité. *Comptes rendus de l'Académie des Sciences, Paris* **182:** 1395–1398.

DeMartonne E. 1926b. Une nouvelle fonction climatologique: l'indice d'aridité. *La Météorologie* **1926:** 449–453.

Doliner LH, Jolliffe PA. 1979. Ecological evidence concerning the adaptive significance of the C_4 dicarboxylic pathway of photosynthesis. *Oecologia* **38:** 23–34.

Eder A, Stichler W, Ziegler H. 1979. Typen der photosynthetischen CO_2-Fixierung bei mitteleuropäischen *Euphorbia*-Arten. *Flora* **168:** 227–240.

Edwards GE, Franceschi VR, Voznesenskaya EV. 2004. Single-cell C_4 photosynthesis versus the dual-cell (Kranz) paradigm. *Annual Reviews of Plant Biology* **55:** 173–196.

Ehleringer JR, Monson RK. 1993. Evolutionary and ecological aspects of photosynthetic pathway variation. *Annual Review of Ecology and Systematics* **24:** 411–439.

Ehleringer JR, Cerling TE, Heliker R. 1996. C_4 photosynthesis, atmospheric CO_2 and climate. *Oecologia* **112:** 285–299.

Ellis RP, Vogel JC, Fuls A. 1980. Photosynthetic pathways and geographical distribution of grasses in South West Africa/Namibia. *South African Journal of Sciences* **76:** 307–314.

Farquhar GD, Ehleringer JR, Hubick KT. 1989a. Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology* **40:** 503–537.

Farquhar GD, Hubick KT, Condon AG, Richards RA. 1989b. Carbon isotope fractionation and plant water-use efficiency. In: Rundel PW, Ehleringer JR, Nagy KA, eds. *Stable isotopes in ecological research. Ecological studies*, Vol. 68. Berlin – Heidelberg – New York: Springer, 21–40.

Funk JL. 2008. Differences in plasticity between invasive and native plants from a low resource environment. *Journal of Ecology* **96:** 1162–1173.

Gamaley YV. 1985. The variations of the Kranz-anatomy in Goby and Karakum desert plants. *Botanicheskii Zhurnal* **70:** 1302–1314 [in Russian].

Gamaley YV, Glagoleva TA, Kolchesvski KG, Chlanovskaja MV. 1972. Ecology and evolution of C_4-syndrome types in relation with phylogeny of families Chenopodiaceae and Poaceae. *Botanicheskii Zhurnal* **77:** 2–12 [in Russian].

Greuter W, Burdet HM, Long G. 1984. *Med-checklist, 1*. Geneva: Conservatoire et Jardin botaniques de la Ville de Genève.

Guehl J-M, Bonal D, Ferhi A, Barigah TS, Farquhar GD, Granier A. 2004. Community level diversity of carbon-water relations in rainforest trees. In: Gourlet-Fleury S, Guehl J-M, Laroussinie O, eds. *Ecology and management of a neotropical rainforest*. Amsterdam: Elsevier, 75–94.

Gutierrez M, Gracen VE, Edwards GE. 1974. Biochemical and cytological relationships in C4 plants. *Planta* **119:** 279–300.

Hattersley PW. 1983. The distribution of C_3 and C_4 grasses in Australia in relation to climate. *Oecologia* **57:** 113–128.

Hattersley PW. 1987. Variations in photosynthetic pathways. In: Sonderstrom RT, Hilu KW, Campbell CS, Barkworth ME, eds. *Grass systematics and evolution*. Washington: Smithsonian Institute Press, 49–64.

Hattersley HA, Watson L. 1992. Diversification of photosynthesis. In: Chapman GP, ed. *Grass evolution and domestication*. Cambridge: Cambridge University Press, 38–116.

Hesla BI, Tieszen LL, Imbamba SK. 1982. A systematic survey of C_3 and C_4 photosynthesis in the Cyperaceae of Kenya, East Africa. *Oecologia* **16:** 196–205.

Kadereit JW. 2008. Evolution und Systematik. *Strasburger Lehrbuch der Botanik*, 36th edn. Heidelberg – Berlin: Spektrum Akademischer Verlag, 557–923.

Kalapos T, Baloghné-Nyakas A, Csontos P. 1997. Occurrence and ecological characteristics of C_4 dicot and Cyperaceae species in the Hungarian flora. *Photosynthetica* **33:** 227–240.

Li M. 1993. Distribution of C_3 and C_4 species of *Cyperus* in Europe. *Photosynthetica* **28:** 119–126.

Li MR, Wedin DA, Tieszen LL. 1999. C-3 and C-4 photosynthesis in *Cyperus* (Cyperaceae) in temperate eastern North America. *Canadian Journal of Botany* **77:** 209–218.

Lüttge U. 2002. CO_2 concentrating: consequences in crassulacean acid metabolism. *Journal of Experimental Botany* **53:** 2131–2142.

Maricle BR, Koteyeva NK, Voznesenskaya EV, Thomasson JR, Edwards GE. 2009. Diversity in leaf anatomy, and stomatal distribution and conductance, between salt marsh and freshwater species in the C4 genus *Spartina* (Poaceae). *New Phytologist* **184:** 216–233.

Mateu AI. 1992. A revised list of the European C_4 plants. *Photosynthetica* **26:** 323–331.

Mateu AI. 1993. Micro-ecology and some related aspects of C_4 plants living in Europe. *Photosynthetica* **29:** 583–594.

Muhaidat R, Sage RF, Dengler NG. 2007. Diversity of Kranz anatomy and biochemistry in C-4 eudicots. *American Journal of Botany* **94:** 362–381.

Müller MJ. 1982. *Selected climate data for a global set of standard stations for vegetation science*. The Hague: W. Junk.

Okuda T, Furukawa A. 1990. Occurrence and distribution of C_4 plants in Japan. *Japan Journal of Ecology* **40:** 91–121.

Park J, Knoblauch M, Okita TW, Edwards GE. 2009. Structural changes in the vacuole and cytoskeleton are key to development of the two cytoplasmic domains supporting single-cell C_4 photosynthesis in *Bienertia sinuspersici*. *Planta* **229:** 369–382.

Pyankov VI, Mokronosov AT. 1993. Basic tendencies in changes of the earth's vegetation in relation to global warming of the climate. *Russian Journal of Plant Physiology* **40:** 443–458.

Pyankov VI, Molotkovskii YI. 1992. Species composition and ecological role of C_4 grasses in the arid zone of Central Asia. *Soviet Journal of Ecology* **23:** 144–151.

Pyankov VI, Molotkovskii YI. 1993. C_4-flora of 'Tiger Valley' reserve, South Tadjikistan. *Proceedings of the Academy Science Tadjikistan* **35:** 38–43 [in Russian].

Pyankov VI, Vakhrusheva DV. 1989. The pathways of primary CO_2 fixation in Chenopodiaceae C_4 plants of

Central Asian arid zone. *Soviet Journal of Plant Physiology* **36:** 178–187.

Pyankov VI, Vakhrusheva DV, Burundukova OL. 1986. The photosynthetic pathway types in the hot desert of Central Karakum and its ecological importance. *Problems of Desert Development* **2:** 45–54 [in Russian].

Pyankov VI, Kuzmin AN, Demidov ED, Maslov AI. 1992a. Diversity of biochemical pathways of CO_2 fixation in plants of the families Poaceae and Chenopodiaceae from arid zone of Central Asia. *Soviet Journal of Plant Physiology* **39:** 411–420.

Pyankov VI, Voznesenskaja EV, Kuzmin AN, Demidov ED, Vasiljev AA, Dzubenko OA. 1992b. C_4-photosynthesis in alpine species of the Pamirs. *Soviet Journal of Plant Physiology* **39:** 421–430.

Pyankov VI, Voznesenskaja EV, Kondratschuk AV, Black CC. 1997. A comparative anatomical and biochemical analysis in *Salsola* (Chenopodiaceae) species with and without a Kranz type leaf anatomy: a possible reversion of C_3 to C_4 photosynthesis. *American Journal of Botany* **84:** 597–606.

Pyankov VI, Artyusheva EG, Edwards G. 1999. Formation of C-4 syndrome in leaves and cotyledons of *Kochia scoparia* and *Salsola collina* (Chenopodiaceae). *Soviet Journal of Plant Physiology* **46:** 452–466.

Pyankov VI, Gunin PD, Tsoog S, Black CC. 2000a. C_4 plants in the vegetation of Mongolia: their natural occurrence and geographical distribution in relation to climate. *Oecologia* **123:** 15–31.

Pyankov VI, Voznesenskaya EV, Kuz'min AN, Ku MSB, Ganko E, Franceschi VR, Black CC, Edwards GE. 2000b. Occurrence of C-3 and C-4 photosynthesis in cotyledons and leaves of *Salsola* species (Chenopodiaceae). *Photosynthesis Research* **63:** 69–84.

Pyankov VI, Artyusheva EG, Edwards GE, Black CC, Soltis PS. 2001. Phylogenetic analysis of tribe Salsoleae (Chenopodiaceae) based on ribosomal ITS sequences: implications for the evolution of photosynthesis types. *American Journal of Botany* **88:** 1189–1198.

Redman RE, Yin L, Wang P. 1995. Photosynthetic pathway types in grassland plant species from Northern China. *Photosynthetica* **31:** 251–255.

Sage RF. 2004. The evolution of C_4 photosynthesis. *New Phytologist* **161:** 341–370.

Sage RF, Pearcy RW. 2000. The physiological ecology of C_4 photosynthesis. In: Leegood RC, Sharkey TD, von Caemmerer S, eds. *Photosynthesis: physiology and metabolism*. Dordrecht: Kluwer Academic Publisher, 497–532.

Sage RF, Li M, Monson RK. 1999. The taxonomic distribution of C_4 photosynthesis. In: Sage RF, Monson RK, eds. *C_4 plant biology*. New York: Academic Press, 551–584.

Sage RF, Sage TL, Pearcy RW, Borsch T. 2007. The taxonomic distribution of C-4 photosynthesis in Amaranthaceae sensu stricto. *American Journal of Botany* **94:** 1992–2003.

Schulze E-D, Ellis R, Schulze W, Trimborn P, Ziegler H. 1996. Diversity, metabolic types and $\delta^{13}C$ carbon isotope ratios in the grass flora of Namibia in relation to growth form, precipitation and habitat correlations. *Oecologia* **106:** 352–369.

Shomer-Ilan AS, Nissenbaum A, Waisel Y. 1981. Photosynthetic pathways and the ecological distribution of the Chenopodiaceae in Israel. *Oecologia* **48:** 244–248.

Sikolia S, Beck E, Kinyamario JI, Onyango JC, Ouma G. 2008. δ^{13} values of the Centrospermeae species and their ecological implications in the semi arid conditions. *International Journal of Botany* **4:** 421–429.

Sonnenberg BJ, Botha CEJ. 1992. An investigation of leaf-blade anatomy and photosynthetic characteristics of four Cyperaceae species from the Albany and Bathurst Districts in the Eastern Cape. *South African Journal of Botany* **58:** 297–303.

Stowe LG, Teeri J. 1978. The geographical distribution of C_4 species of the dicotyledonae in relation to climate. *American Naturalist* **112:** 609–623.

Takeda T, Ueno O, Samejima M, Ontani T. 1995. An investigation for the occurrence of C_4 photosynthesis in the Cyperaceae from Australia. *Botanical Magazine (Tokyo)* **98:** 393–411.

Teeri JA, Stowe LG. 1976. Climatic patterns and the distribution of C_4 grasses in North America. *Oecologia* **23:** 1–12.

Teeri JA, Stowe LG, Livingstone DA. 1980. The distribution of C_4-species of Cyperaceae in North America. *Oecologia* **47:** 307–310.

Tieszen LL, Senyimba MM, Imbamba SK, Troughton JH. 1979. The distribution of C_4 grasses and carbon isotope discrimination along an altitudinal and moisture gradient in Kenya. *Oecologia* **37:** 338–350.

Toderich K, Black CC, Juylova E, Kozan O, Mukimov T. 2007. C3/C4 plants in the vegetation of Central Asia, geographical distribution and environmental adaptation in relation to climate. In: Lal R, Suleimenov M, Stewart BA, Hansen DO, Doraiswamy P, eds. *Climate change and terrestrial carbon sequestration in Central Asia*. Boca Raton: Taylor & Francis, 33–63.

Tutin TG, Burges NA, Chater AO, Edmondson JR, Heywood VH, Moore DM, Valentine DH, Walters SM, Webb DA, eds. 1993. *Flora Europaea*, Vol. 1, 2nd edn. Cambridge: Cambridge University Press.

Tutin TG, Heywood UH, Burges NA, Moore DM, Valentine DH, Walters SM, Webb DA, eds. **1964–1980.** *Flora Europaea*, Vols 1–5. Cambridge: Cambridge University Press.

Ueno O. 1998. Immunogold localization of photosynthetic enzymes in leaves of various C4 plants, with particular reference to pyruvate orthophosphate dikinase. *Journal of Experimental Botany* **49:** 1637–1646.

Ueno O, Takeda T. 1992. Photosynthetic pathways, ecological characteristics and the geographical distribution of the Cyperaceae in Japan. *Oecologia* **89:** 195–203.

Ueno O, Takeda T, Murata T. 1986. C_4 acid decarboxylation enzyme activities of C_4 species possessing different Kranz anatomical types in the Cyperaceae. *Photosynthetica* **20:** 111–116.

Ueno O, Takeda T, Maeda E. 1988. Leaf ultrastructure of

C_4 species possessing different Kranz anatomy types in the Cyperaceae. *Botanical Magazine Tokyo* **98:** 393–411.

Vogel JC, Fuls A, Ellis RP. 1978. The geographical distribution of Kranz-grasses in South Africa. *South African Journal of Science* **74:** 209–215.

Vogel JC, Seely MK. 1977. Occurence of C_4 plants in the central Namib deserts. *Madoqua* **10:** 75–78.

Voznesenskaya EV, Franceschi VR, Kiirats O, Freitag H, Edwards GE. 2001. Kranz anatomy is not essential for terrestrial C_4 photosynthesis. *Nature* **414:** 543–546.

Voznesenskaya EV, Chuong SDX, Kiirats O, Franceschi VR, Edwards GE. 2005a. Evidence that C-4 species in genus *Stipagrostis*, family Poaceae, are NADP-malic enzyme subtype with nonclassical type of Kranz anatomy (stipagrostoid). *Plant Science* **168:** 731–739.

Voznesenskaya EV, Koteyeva NK, Choung SD, Akhani H, Edwards GE, Franceschi VR. 2005b. Differentiation of cellular and biochemical features of the single-cell syndrome during leaf development in *Bienertia cycloptera* (Chenopodiaceae). *American Journal of Botany* **92:** 1784–1795.

Voznesenskaya EV, Chuong SDX, Koteyeva NK, Franceschi VR, Freitag H, Edwards GE. 2007. Structural, biochemical, and physiological characterization of C-4 photosynthesis in species having two vastly different types of Kranz anatomy in genus *Suaeda* (Chenopodiaceae). *Plant Biology* **9:** 745–757.

Winter K. 1981. C_4 plants of high biomass in arid regions of Asia: occurrence of C_4 photosynthesis in Chenopodiaceae and Polygonaceae from the Middle East and USSR. *Oecologia* **48:** 100–106.

Ziegler H. 1994. Stable isotopes in plant physiology and ecology. *Progress in Botany* **56:** 1–24.

Ziegler H, Batanouny KH, Sankhla N, Vyas OP, Stichler W. 1981. The photosynthetic pathway types of some desert plants from India, Saudi Arabia, Egypt and Iraq. *Oecologia* **48:** 93–99.

Ziegler H, Trimborn P. 2000. Typen der photosynthetischen CO_2-Fixierung bei Landpflanzen in Mitteleuropa. *Hoppea* **61:** 43–55.

APPENDIX

C_4 Species of Europe

C_4 species listed in Europe previously by Collins & Jones (1985) are marked with one asterisk (*) and those listed by Mateu (1993) by two asterisks (**). Species and families are named according to Tutin *et al*. (*Flora Europaea*; 1964–1980, 1993) and Greuter, Burdet & Long (*Med-Checklist*, 1984). The new nomenclature for Chenopodiaceae according to Akhani *et al*., 2007 and those of Cyperaceae according to Bruhl & Wilson, 2007 are given in brackets. References for $\delta^{13}C$ analyses, where these are not new measurements published here for the first time, are (1) Akhani & Ghasemkhani 2007; (2) Akhani & Ziegler 2002; (3) Akhani *et al*. 1997; (4) Batanouny *et al*. 1988; (5) Batanouny *et al*. 1991; (6) Bruhl & Wilson 2007; (7) Eder, Stichler & Ziegler 1979; (8) Hesla *et al*. 1982; (9) Kalapos *et al*. (1997); (10) Li 1993; (11) Li, Wedin & Tieszen, 1999; (12) Maricle *et al*., 2009; (13) Pyankov *et al*., 1997; (14) Sage *et al*., 2007; (15) Schulze *et al*., 1996; (16) Shomer-Ilan *et al*., 1981; (17) Sikolia *et al*., 2008; (18) Vogel & Seely, 1977; (19) Voznesenskaya *et al*., 2005a; (20) Winter, 1981; and (21) Ziegler & Trimborn, 2000. Assignment to C_4 biochemical subtype based either on anatomical descriptions and/or biochemical determination are according to (22) H. Akhani & M. V. Lara, unpubl. data; (23) Akhani *et al*., 2009; (24) Carraro *et al*., 1999; (25) Eder *et al*., 1979; (26) Gamaley *et al*., 1972; (27) Gutierrez, Gracen & Edwards, 1974; (28) Hattersley, 1987; (29) Muhaidat, Sage & Dengler, 2007; (30) Pyankov & Vakhrusheva, 1989; (31) Pyankov *et al*., 1992a; (32) Pyankov, Artyusheva & Edwards, 1999; (33) Pyankov *et al*., 2000b; (34) Pyankov *et al*., 2001; (35) Sonnenberg & Botha, 1992; (36) Toderich *et al*., 2007; (37) Ueno, 1998; and (38) Voznesenskaya *et al*., 2007. The subtypes given in quotation marks '. . . .' indicate that the given subtypes have been known in related species of the same genus or related genera. However, a final judgment requires biochemical verification. Many subtypes were reported in Sage *et al*., 1999. Enzymes of malate decarboxylation are NAD-ME, NAD-dependent malic enzyme; NADP-ME, NADP-dependent malic enzyme; PEPCK, phospho*enol*pyruvate-carboxykinase. Types of Kranz anatomy are: ARIST, aristidoid; ATR, atriplecoid; BIEN, bienertioid (single-cell); CHLOR, chloridoid; CYPER, chlorocyperoid; KOCH, kochioid; PANIC, panicoid; SALS, salsoloid; SCH, schoberia-type; STIP, stipagrostoid; SUE, suaedoid; N, native; I, invasive. For references, see list in the main text.

Taxa	N/I	$\delta^{13}C$ (‰)	Reference of $\delta^{13}C$ values	Reaction of malate decarboxylation and reference ( )	Type of Kranz anatomy
Amaranthaceae†					
*Alternanthera pungens** Kunth	I	−12.3	(14)	'NAD-ME'	ATR
Alternanthera caracasana Kunth	I	−14.4	(14)	'NAD-ME'	ATR
Alternanthera nodiflora R.Br.	I	−13.6	(14)	'NAD-ME'	ATR
Amaranthus acutilobus Uline & Bray	I	−13.3	(14)	'NAD-ME'	ATR
*Amaranthus albus** L.	N	−12.3, −15.9	(21)	'NAD-ME'	ATR
*Amaranthus blitoides** S.Watson	I	−13.9		'NAD-ME'	ATR
*Amaranthus caudatus** L.	I	−11.7	(21)	'NAD-ME'	ATR
		−13.7			
		−14.1			
Amaranthus crispus (Lesp. & Thév.) N.Terracc.	I	−13.1	(14)	'NAD-ME'	ATR
*Amaranthus cruentus** L. (=*A. patulus** Bertol., *A. paniculatus** L.)	I	−11.2		'NAD-ME'	ATR
		−14.1			
Amaranthus deflexus *L.	N	−12.9		'NAD-ME'	ATR
*Amaranthus graecizans** L.	N	−12.2	(21)	'NAD-ME'	ATR
		−11.1			
*Amaranthus hybridus** L. (=*A. chlorostachys* Willd.)	I	−14.0	(21)	'NAD-ME'	ATR
		−13.4			
*Amaranthus hypochondriacus** L.		−12.2	(14)	'NAD-ME'	ATR
*Amaranthus lividus** L. (=*A. blitum*)	N	−15.0	(9, 21)	'NAD-ME'	ATR
		−18.0			
Amaranthus muricatus (Gillies ex Moq.) Hieron.	I	−12.7	(14)	'NAD-ME'	ATR
Amaranthus palmeri S.Watson	I	−12.5		'NAD-ME'	ATR
Amaranthus polygonoides L.	I	−13.1	(14)	'NAD-ME'	ATR
Amaranthus powellii S. Watson (=*A. bouchonii* Thell.)	I	−13.6	(14)	'NAD-ME'	ATR
Amaranthus quitensis Kunth	I	−12.1	(14)	'NAD-ME'	ATR
*Amaranthus retroflexus** L.	N,I	−11.8	(21)	NAD-ME (29)	ATR
		−15.0			
Amaranthus spinosus L.	I	−13.7		'NAD-ME'	ATR
Amaranthus standleyanus Parodi ex Covas	I	−13.2	(14)	'NAD-ME'	ATR

APPENDIX *Continued*

Taxa	N/I	$\delta^{13}C$ (‰)	Reference of $\delta^{13}C$ values	Reaction of malate decarboxylation and reference ( )	Type of Kranz anatomy
Amaranthus viridis L.	I	–11.7		'NAD-ME'	ATR
Chenopodiaceae					
Anabasis aphylla L.	N	–12.4 –14.5	(3)	NADP-ME (36)	SALS
*Anabasis articulata** (Forssk.) Moq.	N	–12.4	(3)	'NADP-ME'	SALS
Anabasis cretacea Pall.	N			'NADP-ME'	SALS
Anabasis salsa (C.A.Mey.) Benth. ex Volkens	N	–11.6	(3)	NADP-ME (36)	SALS
Atriplex glauca L.	N	–12.9	(3)	'NAD-ME'	ATR
*Atriplex halimus** L.	N	–14.2	(3)	'NAD-ME'	ATR
*Atriplex laciniata** L.	N	–11.4 –11.7	(3, 21)	'NAD-ME'	ATR
Atriplex patens (Litv.) Iljin	N			'NAD-ME'	ATR
Atriplex recurva d'Urv.	N	–12.1	(3)	'NAD-ME'	ATR
*Atriplex rosea** L.	N	–13.5	(3)	NAD-ME (29)	ATR
*Atriplex tatarica** L.	N	–13.7	(3)	NAD-ME (31)	ATR
*Bassia hyssopifolia** (Pall.) Kuntze	N	–12.9 –13.4	(13, 20)	NADP-ME (30)	KOCH
Bassia laniflora (S.G.Gmel.) A.J.Scott	N	–11.4 –14.9	(3)	'NADP-ME'	KOCH
Bassia prostrata (L.) A.J.Scott	N	–13.4 –14.0	(3) (13)	NADP-ME (30, 34)	KOCH
*Bassia scoparia** (L.) A.J.Scott	I	–13.4 –14.5 –13.7	(1, 16)	NADP-ME (29, 32, 34)	KOCH
Bienertia cycloptera Bunge ex Boiss.	N	–14.2 –15.4	(1, 20)	NAD-ME (23)	BIEN
Camphorosma annua Pall.	N	–12.5	(3)	'NADP-ME'	KOCH
Camphorosma monspeliaca L.	N	–13.5 –15.5	(1, 3)	NADP-ME (31, 34)	KOCH
Camphorosma songorica Bunge	N			'NADP-ME'	KOCH
Girgensohnia oppositiflora (Pall.) Fenzl	N	–13.2	(3)	NADP-ME (30, 34)	SALS
Halimocnemis sclerosperma (Pall.) C.A.Mey.	N			'NAD-ME' (23)	SALS
*Halogeton glomeratus** (M. Bieb.) C.A.Mey.	N	–11.3 –12.8	(3)	NADP-ME (31)	SALS
Halogeton sativus (L.) Moq.	I	–11.4	(3)	'NADP-ME'	SALS
Haloxylon tamaricifolium (L.) Pau	N	–12.3	(3)		SALS
Nanophyton erinaceum (Pall.) Bunge	N	–13.5	(3)		SALS
Noaea mucronata (Forssk.) Aschers & Schweinf.	N	–14.1 –15.1	(1, 3)	'NADP-ME' (22)	SALS
Ofaiston monandrum (Pall.) Moq.	N	–13.1	(3)	'NAD-ME'	SALS
Petrosimonia brachiata (Pall.) Bunge	N	–13.4 –13.7	(1, 3)	NAD-ME (26)	SALS
Petrosimonia brachyphylla (Bunge) Iljin	N			'NAD-ME'	SALS
Petrosimonia glaucescens (Bunge) Iljin	N			'NAD-ME' (26)	SALS
Petrosimonia litwinowii Korsh.	N			'NAD-ME'	SALS
Petrosimonia monandra (Pallas) Bunge	N			'NAD-ME'	SALS
Petrosimonia oppositifolia (Pall.) Litv.	N	–11.9	(3)	'NAD-ME'	SALS
Petrosimonia triandra (Pall.) Simonk.	N			'NAD-ME'	SALS
Salsola acutifolia (Bunge) Botsch.	N				SALS
Salsola aegaea Rech. f. (*Caroxylon aegeum* (Rech.f.) Akhani & E.H.Roalson)	N	–12.5		'NAD-ME'	SALS
Salsola affinis C.A.Mey. (*Climacoptera affinis* (C.A.Mey.) Botsch.)	N	–11.3	(3)	'NAD-ME'	SALS
Salsola arbuscula Pall. (*Xylosalsola arbuscula* (Pall.) Tzvelev)	N	–12.4 –11.4 –13.0	(3) (13)	NADP-ME (34)	SALS
Salsola brachiata Pall. (*Pyankovia brachiata* (Pall.) Akhani & E.H.Roalson)	N	–12.2 –13.4 –15.2	(1, 3, 20)	'NAD-ME'	SALS

APPENDIX *Continued*

Taxa	N/I	$\delta^{13}C$ (‰)	Reference of $\delta^{13}C$ values	Reaction of malate decarboxylation and reference ( )	Type of Kranz anatomy
Salsola carpatha P.H.Davis (*Caroxylon carpathum* (P.H.Davis) Akhani & E.H.Roalson)	N	–15.1	(3)	'NAD-ME'	SALS
Salsola collina Pall.‡	I	–11.6	(3)	NADP-ME (31, 32)	SALS
Salsola crassa M.Bieb. (*Climacoptera crassa* (M.Bieb.) Botsch.)	N	–11.0	(3)	NAD-ME (30)	SALS
*Salsola dendroides*** Pall. (*Caroxylon dendroides* (Pall.) Tzvelev)	N	–13.9	(3, 13, 20)	NAD-ME (34)	SALS
		–12.9			
		–13.9			
Salsola foliosa (L.) Schrad.	N	–12.0	(3)		SALS
		–11.1			
*Salsola kali** L.‡	N	–11.1	(3)	NADP-ME (27, 34)	SALS
Salsola lanata Pall. (*Climacoptera lanata* (Pall.) Botsch.)	N	–14.6	(3)	NAD-ME (30, 34)	SALS
Salsola laricina Pall. (*Caroxylon laricinum* (Pall.) Tzvelev)	N	–13.2		NAD-ME (33)	SALS
Salsola melitensis Botsch.	N				SALS
Salsola nitraria Pall. (*Caroxylon nitrarium* (Pall.) Akhani & E.H.Roalson)	N	–13.3	(1, 20)	'NAD-ME'	SALS
		–12.6			
Salsola nodulosa (Moq.) Iljin (*Caroxylon verrucosum* Moq.)	N			'NAD-ME'	SALS
Salsola oppositifolia Desf.	N	–11.1	(3)	'NADP-ME'	SALS
Salsola papillosa (Coss.) Willk.	N	–13.1	(3)	'NAD-ME'	SALS
Salsola paulsenii Litv.‡	N	–12.3	(3)	NADP-ME (33)	SALS
Salsola pellucida Litv.	N	–11.3	(20)	'NADP-ME'	SALS
Salsola soda L.	N	–11.8	(3)	'NADP-ME'	SALS
Salsola tamariscina Pall.	N	–11.8	(3)		SALS
Salsola turcomanica Litv. (*Climacoptera turcomanica* (Litv.) Botsch.)	N	–13.3	(3)	'NAD-ME'	SALS
*Salsola vermiculata*** L. (*Caroxylon vermiculatum* (L.) Akhani & E.H.Roalson)	N	–13.3	(3)	NAD-ME (22)	SALS
Suaeda altissima (L.) Pall.	N	–13.3	(3)	NAD-ME (26)	SUE
Suaeda baccifera Pall.	N	–10.7		'NAD-ME'	SCH
Suaeda confusa Iljin	N	–10.5	(3)	NAD-ME (29)	SCH
Suaeda dendroides (C.A.Mey.) Moq.	N	–12.3	(3)	'NAD-ME'	SUE
Suaeda eltonica Iljin	N	–11.8		NAD-ME (38)	SCH
Suaeda splendens (Pourr.) Gren. & Godr.	N	–13.4		'NAD-ME'	SCH
Suaeda pruinosa Lange	N	–13.7		NAD-ME (29)	SUE
Euphorbiaceae					
*Euphorbia chamaesyce** L.	N	–13.1	(5)	'NADP-ME'	ATR
		–14.0			
Euphorbia humifusa L.	N	–13.6	(7)	NADP-ME (25)	ATR
*Euphorbia maculata** L.	I	–15.0, –17.3	(7, 8)	NADP-ME (24, 25)	ATR
*Euphorbia nutans** Lag.	I	–11.3		'NADP-ME'	ATR
*Euphorbia peplis** L.	N	–11.8	(5)	'NADP-ME'	ATR
		–14.1			
*Euphorbia poligonifolia** L.	I	–13.4		'NADP-ME'	ATR
*Euphorbia prostrata*** Aiton	I	–12.1	(5)	'NADP-ME'	ATR
*Euphorbia serpens** Kunth	I			'NADP-ME'	ATR
Nyctaginaceae					
Boerhavia repens L.	I			'NADP-ME' (29)	ATR
Polygonaceae					
Calligonum aphyllum (Pall.) Gürke	N			'NAD-ME' (29)	SALS
Portulacaceae					
*Portulaca grandiflora** Hook.	I	–12.3	(17)	NADP-ME (29)	ATR
*Portulaca oleracea** L.	I	–14.9	(17)	NAD-ME (29)	ATR
Zygophyllaceae					
*Tribulus terrestris** L.	N	–13.9	(9)	'NADP-ME' (29)	ATR
Cyperaceae					
Cyperus auricomus Sieber ex Spreng. (*C. digitatus* Roxb. subsp. *auricomus* (Sieb. ex Spreng.) Kuk.)	I	–13.0	(10)	'NADP-ME'	CYPER
*Cyperus brevifolius** (Rottb). Hassk. (*Kyllinga brevifolia* Rottb.)	I	–10.8	(6)	'NADP-ME'	CYPER
*Cyperus capitatus** Vand.	N	–12.3		'NADP-ME'	CYPER

APPENDIX *Continued*

Taxa	N/I	$\delta^{13}C$ (‰)	Reference of $\delta^{13}C$ values	Reaction of malate decarboxylation and reference ( )	Type of Kranz anatomy
Cyperus congestus Vahl	I	–9.6 –13.0	(6, 10)	NADP-ME (35)	CYPER
Cyperus echinatus (L.) Alph. (= *C. ovularis* (Michx.) Torr.)	N	–14.0	(10)	'NADP-ME'	CYPER
*Cyperus esculentus** L.	N	–11.3 –12.7	(11)	'NADP-ME'	CYPER
Cyperus flavescens L. (*Pycreus flavescens (L.)* Rchb.)		–11.6 –11.3 –10.1	(9, 21)		
*Cyperus flavidus*** Retz. (*Pycreus flavidus* (Retz.) T.Koyama)	N	–11.8	(10)	'NADP-ME'	CYPER
Cyperus glaber L.		–11.7	(9)	'NADP-ME'	CYPER
Cyperus glomeratus L.		–12.8	(9)	'NADP-ME'	CYPER
Cyperus hamulosus M.Bieb.	N	–12.4	(10)	'NADP-ME'	CYPER
*Cyperus laevigatus** L.	N	–8.8		'NADP-ME'	CYPER
*Cyperus longus** L.	N	–12.8		'NADP-ME'	CYPER
Cyperus michelianus (L.) Link.	N	–10.0 –10.7	(9, 21)	'NADP-ME'	CYPER
Cyperus mundtii (Nees) Kunth (*Pycreus mundtii* Nees)	I	–12.3 –12.0	(6)	'NADP-ME'	CYPER
Cyperus pannonicus Jacq.	I	–10.7		'NADP-ME'	CYPER
*Cyperus papyrus** L.	I	–11.4		'NADP-ME'	CYPER
*Cyperus polystachyos** Rottb. (*Pycreus polystachyos* (Rottb.) P.Beauv.)	N	–11.0		'NADP-ME'	CYPER
*Cyperus rotundus** L.	N	–11.2		'NADP-ME'	CYPER
*Cyperus serotinus** Rottb.	N	–9.9	(9)	'NADP-ME'	CYPER
Cyperus squarrosus L.	I	–10.9	(11)	'NADP-ME'	CYPER
Cyperus strigosus L.	N	–10.1	(11)	'NADP-ME'	CYPER
*Fimbristylis annua*** (All.) Roem. & Schult.	N	–9.7		'NADP-ME'	FIMBR
*Fimbristylis bisumbellata** (Forssk.) Bubani	N	–13.7	(8)	'NADP-ME'	FIMBR
Fimbristylis cioniana Savi (*Bulbostylis cioniana* (Savi) Lye)	I	–11.0		'NADP-ME'	FIMBR
*Fimbristylis ferruginea** (L.) Vahl	I	–11.6	(6)	'NADP-ME'	FIMBR
Fimbristylis squarrosa Vahl	I	–9.8		'NADP-ME'	FIMBR
Poaceae					
*Aeluropus lagopoides*** (L.) Trin. ex Thwaites	N	–13.3		NAD-ME	CHLOR
*Aeluropus littoralis*** (Gouan) Parl.	N	–14.1 –14.7	(2, 4)	NAD-ME (31)	CHLOR
Andropogon distachyos L.	N	–12.0	(4)	NADP-ME (28)	PANIC
*Aristida adscensionis** L.	N	–12.8 –13.9	(15)	NADP-ME (22)	ARIST
*Brachiaria eruciformis** (Sibth. & Sm.) Griseb.	N	–11.1		PEPCK	CHLOR
*Cenchrus ciliaris** L.	I	–12.3	(15)	NADP-ME	PANIC
*Cenchrus incertus** M.A. Curtis	I			NADP-ME (28)	PANIC
Cenchrus longispinus (Hack.) Fernald	I			NADP-ME	PANIC
*Chrysopogon gryllus** (L.) Trin.	N			NADP-ME	PANIC
Cleistogenes serotina (L.) Keng	N	–13.3 –14.3	(2)	NAD-ME	CHLOR
Cleistogenes squarrosa (Trin.) Keng	N	–14.4 –16.4		NAD-ME	CHLOR
*Coix lacryma-jobi** L.	I			NADP-ME	
Crypsis aculeata (L.) Aiton	N	–11.5 –11.9 –13.1		NAD-ME or PEPCK	CHLOR
Crypsis acuminata Trin.	N			NAD-ME or PEPCK	CHLOR
Crypsis alopecuroides (Piller & Mitterp.) Schrad.	N	–13.1		NAD-ME or PEPCK	CHLOR
Crypsis schoenoides (L.) Lam.	N	–11.9 –12.9	(2)	NAD-ME or PEPCK	CHLOR

APPENDIX *Continued*

Taxa	N/I	$\delta^{13}C$ (‰)	Reference of $\delta^{13}C$ values	Reaction of malate decarboxylation and reference ( )	Type of Kranz anatomy
Crypsis turkestanica Eig	N			NAD-ME or PEPCK	CHLOR
*Cynodon dactylon** (L.) Pers.	N	–15.6 –13.9 –14.5	(2, 4, 21)	NAD-ME (31, 28)	CHLOR
*Dactylostemium aegypticum** (L.) Beauv.	I	–11.3	(15)	PEPCK	CHLOR
Dichantium insculptum (A.Rich.) Clayton	N			NADP-ME	PANIC
*Dichantium ischaemum** (L.) Roberty	N	–12.8 –11.3	(2, 21)	NADP-ME	PANIC
Digitaria ciliaris (Retz.) Koehler	I	–10.1		NADP-ME	PANIC
Digitaria debilis (Desf.) Willd.	I	–11.4	(15)	NADP-ME	PANIC
*Digitaria ischaemum*** (Schreb.) Muhl.	N	–12.5	(21)	NADP-ME	PANIC
*Digitaria sanguinalis** (L.) Scop.	N	–11.2 –11.9	(4, 15, 21)	NADP-ME (28)	PANIC
*Echinochloa colona** (L.) Link.	I	–11.9		NADP-ME	PANIC
*Echinochloa crus-galli** (L.) P.Beauv.	I	–11.1 –16.2	(15, 21)	NADP-ME (28, 37)	PANIC
Echinochloa oryzoides (Ard.) Fritsch	I			NADP-ME	PANIC
Eleusine coracana (L.) Gaertn.	I			NAD-ME (28)	PANIC
*Eleusine indica** (L.) Gaertn.	I	–16.3	(15)	NAD-ME (28)	CHLOR
*Eleusine tristachya** (Lam.) Lam.	I			NAD-ME	CHLOR
Enneapogon persicus Boiss.	N			NAD-ME	CHLOR
Eragrostis aegyptiaca (Willd.) Link	N			NAD-ME	CHLOR
*Eragrostis barrelieri** Daveau	N	–12.7 –13.9		NAD-ME	CHLOR
*Eragrostis cilianensis** (All.) F.T.Hubbard	N	–15.4 –14.3 –11.7	(4, 15, 21)	NAD-ME (28)	CHLOR
Eragrostis collina Trin.	N			NAD-ME	CHLOR
Eragrostis diarrhena (Schult. & Schult.f.) Steud.	N			NAD-ME	CHLOR
Eragrostis japonica (Thunb.) Trin.	I			NAD-ME	CHLOR
*Eragrostis minor*** Host	N	–13.9 –14.3	(2, 21)	NAD-ME (28)	CHLOR
*Eragrostis papposa** (Dufour) Steud.	N			NAD-ME	CHLOR
Eragrostis pectinacea (Michx.) Nees ex Steud.	I			NAD-ME	CHLOR
Eragrostis pilosa (L.) P.Beauv.	N	–15.0 –15.1	(4, 15, 21)	NAD-ME	CHLOR
*Eragrostis tef** (Zucc.) Trotter	I	–16.3		NAD-ME	CHLOR
Eriochloa succinata (Trin.) Kunth	N			PEPCK (28)	CHLOR
Eriochloa villosa (Thunb.) Kunth	N			PEPCK (28)	CHLOR
Hemarthria altissima (Poir.) Stapf & C.E.Hubbard	N	–12.2 –12.4	(4) (15)	NADP-ME	PANIC
*Heteropogon contortus** (L.) P.Beauv. ex Roem. & Schult.	N	–12.1 –12.9	(2, 15)	NADP-ME	PANIC
*Hyparrhenia hirta*** (L.) Stapf	N	–12.6 –13.0	(15)	NADP-ME (28)	PANIC
*Imperata cylindrica** (L.) Raeusch.	N	–11.1 –12.2 –13.5	(2, 4, 15)	NADP-ME (31)	PANIC
*Panicum capillare** L.	I	–14.1	(21)	NAD-ME (28)	PANIC
*Panicum dichotomiflorum*** Michx.	I	–13.4		NAD-ME (28, 37)	PANIC
Panicum implicatum Scribn. ex Britton & A.Br.					PANIC
*Panicum maximum** Jacq.	N	–13.3 –12.8	(4, 15)	PEPCK (28, 37)	PANIC
*Panicum miliaceum** L.	I	–13.5	(21)	NAD-ME (28)	PANIC
*Panicum repens** L.	N	–12.5	(15)	NAD-ME	PANIC
*Paspalum dilatatum** Poir.	I			NADP-ME (28)	PANIC
*Paspalum paspaloides*** (Michx.) Scribn.	I	–10.3	(4)	NADP-ME	PANIC

APPENDIX *Continued*

Taxa	N/I	$\delta^{13}C$ (‰)	Reference of $\delta^{13}C$ values	Reaction of malate decarboxylation and reference ( )	Type of Kranz anatomy
*Paspalum urvillei*** Steud.	I			NADP-ME	PANIC
*Paspalum vaginatum** Sw.	I	–12.8	(15)	NADP-ME	PANIC
*Pennisetum setaceum** (Forssk.) Chiov.	N	–12.6	(4)	NADP-ME	PANIC
*Pennisetum villosum** R.Br. ex Fresen.	N			NADP-ME	PANIC
Phacelurus digitatus (Sibth. & Sm.) Griseb.	N			NADP-ME	PANIC
*Saccharum officinarum** L.	I			NADP-ME (28).	PANIC
*Saccharum ravennae*** (L.) Murray	N			NADP-ME (31)	PANIC
*Saccharum spontaneum** L.	I	–11.7		NADP-ME	PANIC
Saccharum strictum (Host) Spreng.	N			NADP-ME	PANIC
*Setaria geniculata** (Lam.) P.Beauv.	I			NADP-ME	PANIC
*Setaria italica** (L.) Beauv.	I	–11.1 –14.4	(4, 21)	NADP-ME (28)	PANIC
*Setaria pumila*** (Poir.) Schult.	N	–11.9	(21)	NADP-ME	PANIC
*Setaria verticillata** (L.) Beauv.	N	–13.6 –12.0	(4, 21)	NADP-ME (28)	PANIC
*Setaria viridis** (L.) Beauv.	N	–13.4 –11.6 –12.9	(2, 4, 15, 21)	NADP-ME (28, 31)	PANIC
*Sorghum bicolor** (L.) Moench	I	–12.4		NADP-ME (28, 37)	PANIC
*Sorghum halepense** (L.) Pers.	I	–12.0 –13.1	(2, 15)	NADP-ME	PANIC
*Sorghum sudanense** (Piper) Stapf	I			NADP-ME (28)	PANIC
*Spartina alterniflora** Loisel.	I	–14.5	(12)	'PEPCK'	
Spartina anglica C.E.Hubb.	N	–13.7	(12)	PEPCK (28)	
*Spartina densiflora*** Brongn.	I	–14.3	(12)	'PEPCK'	
*Spartina maritima** (Curtis) Fernald	N	–12.7	(15, 21)	PEPCK	PANIC
*Spartina townsendii** H.Groves & J.Groves	N	–12.0	(21)	PEPCK	
*Spartina versicolor*** E. Fabre	N	–12.4		PEPCK	
*Sporobolus indicus** (L.) R.Br.	I			PEPCK (37)	CHLOR
*Sporobolus pungens*** (Schreb.) Kunth	N				CHLOR
*Stenotaphrum secundatum** (Walter) Kuntze	I			NADP-ME	PANIC
Stipagrostis karelinii (Trin. & Rupr.) Tzvelev	N			NADP-ME	STIPA
Stipagrostis pennata (Trin.) DeWinter	N	–14.4	(19)	NADP-ME (38)	STIPA
Tragus racemosus (L.) All.	N	–12.3 –12.5	(15, 21)	NAD-ME	CHLOR
*Tricholaena teneriffae** (L.f.) Link	N	–13.4	(4)	PEPCK	CHLOR
*Zea mays** L.	I	–13.3	(21)	NADP-ME (28, 31, 37)	PANIC

†Genera from *Anabasis* to *Suaeda*, inclusive, are now generally included in Amaranthaceae (APG III, 2009).
‡In Akhani *et al*. (2007), the species of *Salsola* section *Kali* were transferred to the genus *Kali*. We have since discovered that *Kali* is a nomenclatural synonym of *Salsola* and therefore cannot be considered as a different genus. A nomenclatural solution to this is now under revision (H. Akhani).